Live birth in Cretaceous marine lizards (mosasauroids)

Michael W. Caldwell[1*] and Michael S. Y. Lee[2,3]

[1]*Department of Earth and Atmospheric Sciences, and Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E3*
[2]*Department of Zoology, The University of Queensland, Brisbane 4072, Australia*
[3]*The South Australian Museum, North Terrace, Adelaide 5000, Australia*

Although live-bearing (viviparity) has evolved around 100 times within reptiles, evidence of it is almost never preserved in the fossil record. Here, we report viviparity in mosasauroids, a group of Cretaceous marine lizards. This is the only known fossil record of live-bearing in squamates (lizards and snakes), and might represent the oldest occurrence of the trait in this diverse group; it is also the only known fossil record of viviparity in reptiles other than ichthyosaurs. An exceptionally preserved gravid female of the aigialosaur *Carsosaurus* (a primitive mosasauroid) contains at least four advanced embryos distributed along the posterior two-thirds of the long trunk region (dorsal vertebrae 9–21). Their orientation suggests that they were born tail-first (the nostrils emerging last) to reduce the possibility of drowning, an adaptation shared with other highly aquatic amniotes such as cetaceans, sirenians and ichthyosaurs; the orientation of the embryos also suggests that they were not gut contents because swallowed prey are usually consumed head-first. One embryo is located within the pelvis, raising the possibility that the adult died during parturition. Viviparity in early medium-sized amphibious aigialosaurs may have freed them from the need to return to land to deposit eggs, and permitted the subsequent evolution of gigantic totally marine mosasaurs.

Keywords: mosasauroids; viviparity; aigialosaurs; squamates

1. INTRODUCTION

The mosasauroids (Mosasauroidea) are a diverse Cretaceous radiation of marine lizards that include the primitive medium-sized aigialosaurs (Aigialosauridae) and the derived gigantic mosasaurs (Mosasauridae) (Carroll & deBraga 1992; deBraga & Carroll 1993; Bell 1997). The aigialosaur *Carsosaurus marchesetti* is known from a single specimen collected from the Trieste limestone (Cenomanian–Turonian, mid-Cretaceous) near Komen, Slovenia (Kornhuber 1893; Calligaris 1988; Caldwell *et al.* 1995). *Carsosaurus* is the largest aigialosaur known (*ca.* 2 m in total length) and has proportionally larger limbs than the aigialosaurs *Aigialosaurus*, *Opetiosaurus* and the 'Trieste aigialosaur' (Carroll & deBraga 1992; Caldwell *et al.* 1995). The postcranial skeleton, exposed in ventral view, is very complete and perfectly articulated, but unfortunately the skull is missing, making comparisons with other aigialosaur specimens with skulls impossible.

Kornhuber's (1893) original description of the type of *C. marchesetti* noted the preservation of soft-body details such as scales, and also the presence of small vertebrate skeletal elements in the body cavity of the trunk region (e.g. jaw tips with teeth). However, Kornhuber (1893) interpreted these extra skeletal elements to be gut contents.

We re-examined *C. marchesetti* while visiting numerous collections in southern Europe in the spring of 1996. Our first impression was that these extra skeletal elements were not gut contents, but rather represented the well-preserved remains of multiple embryos contained within the body cavity. Detailed re-analysis of the specimen

during the summer of 1999 confirmed this suspicion. Here, we present new data detailing the anatomy of at least four embryos of the poorly known aigialosaur *C. marchesetti*. This Cretaceous marine lizard is remarkable for two reasons. First, although live-bearing (viviparity) has evolved around 100 times within reptiles (Blackburn 1982, 1985; Shine 1985), evidence of viviparity is almost never preserved in the fossil record. Second, viviparity in the marine aigialosaurs suggests that the more derived members of the clade, the mosasaurs, may also have been viviparous. We suggest that viviparity was an important reproductive capability that facilitated the aquatic radiation of this large and diverse group of marine lizards.

2. METHODS

Photographs were taken of the original specimen using a Nikon camera and close-up lenses. Drawings were made directly from the original specimen (holotype of *C. marchesetti*, Museo Civico di Storia Naturale, Trieste, Italy, unnumbered) and from high-quality latex peels made from a silicone mold. Reconstructions of embryos and adults of *C. marchesetti* are based on drawings and photographs of the entire specimen.

3. DESCRIPTIONS

Abundant remains of advanced embryos preserved within the body cavity of *Carsosaurus* indicate that this individual is a gravid female close to parturition. The presence of at least four small lizards within the body cavity can be inferred from the presence of four pairs of jaws (figure 1). An extra pair of mandible-like elements might represent another individual (figure 1). These
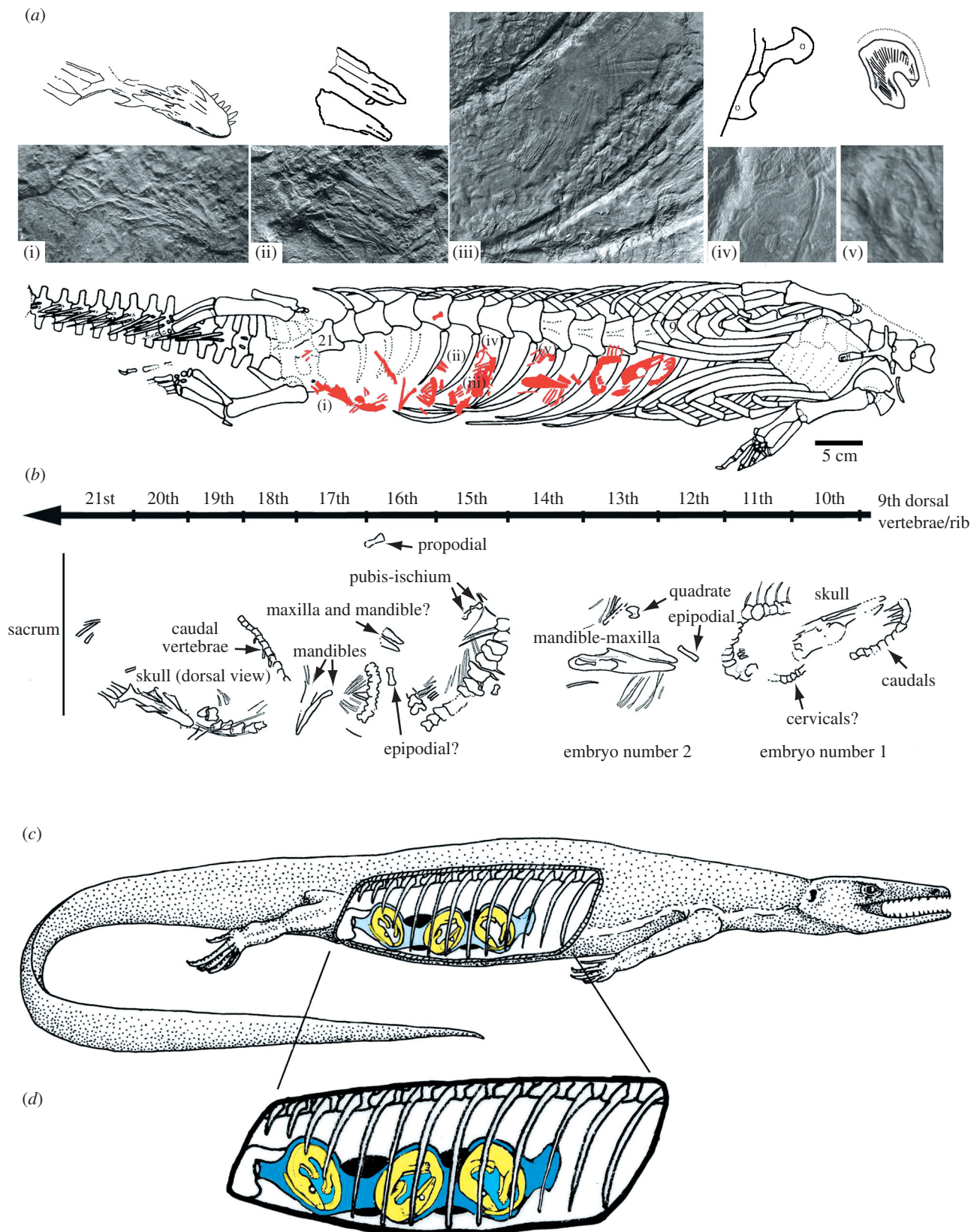
Figure 1. (*a*) Photographs and line drawings of embryonic skeletal elements: (i) skull in dorsal view; (ii) maxilla and mandible in lateral view; (iii) articulated vertebral column and ribs; (iv) pelvic elements; and (v) probable quadrate. (*b*) Adult skeleton of *Carsosaurus marchesetti*, showing the locations of the embryonic skeletal components (highlighted in red), with roman numerals i–v indicating the positions of the photographed elements. (*c*) Detailed drawings of all the embryonic material in shown in (*b*). (*d*) Reconstruction of the adult and three embryos of the right oviduct.

individuals are all aigialosaurs (based on vertebral and limb element characters) and are of the same size class. They are preserved in natural position and natural posture. Their even spacing along the body cavity reflects their positions within the elongated oviducts. The most anterior (embryo number 1) is preserved between the ninth and 12th dorsal ribs, with the most posterior located between the 18th and 21st dorsal ribs. The curled-up posture of the embryos (suggested by the articulated vertebral series of embryo number 1) is typical of viviparous squamates, where the embryos are encased in amniotic membranes. The number of embryos preserved in close proximity often makes the attribution of elements to particular embryos impossible. The exceptions are the two anterior-most embryos (numbers 1 and 2), which are well articulated and also separated from the main mass of elements.

Embryo number 1 is very complete. The skull is exposed in left lateral view, but is upside down, so that the dorsal surface faces the ventral surface of the adult. The snout, with identifiable maxilla, dentary and a probable splenial, overlies the 10th dorsal rib. The ventral margins of the orbit are clearly visible, while the dorsal margins are somewhat obscured by a thin layer of sediment. However, the orbit is clearly proportionately very large, as in most embryos and neonates. Fragments of the temporal region are preserved, but precise identities cannot be made. Posterior to the skull, overlying the 11th dorsal rib, are 14 articulated dorsal vertebrae and ribs. The ribs are very thin at this developmental stage, and only lightly ossified. Anterior to the skull 11 proximal caudal vertebrae are preserved. The six or seven small vertebrae located immediately below the temporal region of the skull probably represent distal caudal vertebrae (the alternative interpretation as cervical vertebrae is less likely due to their small size). A small epipodial (probably radius or ulna) near the main vertebral series probably belongs to this embryo.

Embryo number 2 consists mainly of a complete lower jaw and partial upper jaw, exposed in right lateral view. Though suture lines are not identifiable, a dentary, coronoid and surangular are visible, as is a vertical intra-mandibular joint typical of mosasauroids. A distinctive circular quadrate (figure 1a(v)), again typical of mosa-sauroids, lies nearby, and is probably part of the same skull. The postcranial skeleton is not well exposed due to the presence of a very thin layer of matrix; however, numerous ribs are visible.

The remaining preserved clusters of elements cannot be assigned confidently to particular embryos because of the density of material. A series of 14 dorsal vertebrae bearing long and well-preserved ribs overlies the 15th dorsal rib of the adult (figure 1a(iii)). Pelvic elements (left and right pubes) are preserved at the posterior end of this juvenile vertebral series (figure 1a(iv)); these pubes show a well-developed symphysis and pubic fenestra. Three small (possibly cervical) vertebrae are visible near the other end of this series. Continuing posteriorly, a small epipodial, the anterior tip of a pair of jaw elements and a string of numerous small vertebrae and ribs are visible between the 16th and 17th dorsal ribs. A propodial element (humerus or femur) is positioned against the neural arch of the 17th dorsal vertebra, indicating at least slight taphonomic disturbance.
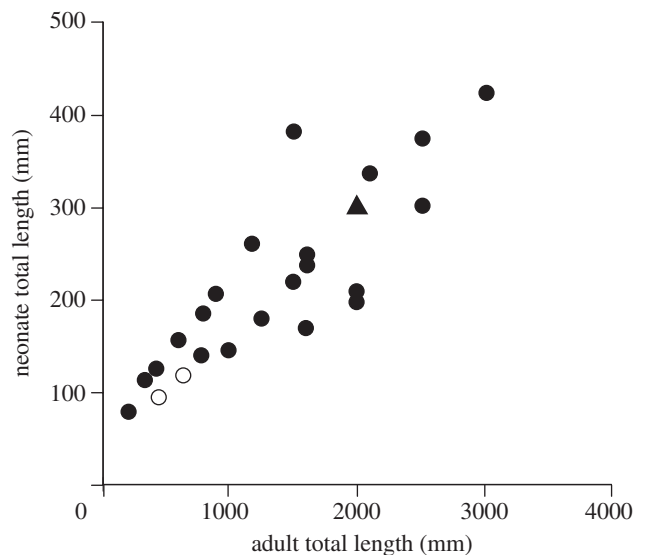
Figure 2. Lengths of adults and neonates of living varanoid lizards: *Varanus* (filled circles) (data from DeLisle 1996); *Heloderma* (open circles) (data from Bogert & del Campo 1956). The estimated total lengths of the adult and embryos of *Carsosaurus* is also indicated (filled triangle), showing that the retained embryos are already as large as the free-living neonates of extant varanoids.

Posterior to the 17th rib are a pair of mandible-like elements, exposed in ventral view and pointing ventrally. Two strings of vertebrae and ribs are positioned behind these. The more dorsal series shows a morphology typical of caudal vertebrae in aigialosaurs: the centrum bodies are small, and bear short posteriorly located haemal arches. The more ventral series consists of larger vertebrae and shows procoelous centra characteristic of squamates.

A large, well-ossified and very complete skull is preserved at the end of the series, overlapping the pelvis of the adult. It is exposed in dorsal view and the visible elements include the premaxilla and maxilla, together with nasal, prefrontal, frontal, palpebral, postorbito-frontal and parietal elements. The sutures are indistinct, but these elements can be identified by shape and relative position. Five long, sharp and widely spaced maxillary teeth are visible. The body of this embryo would have extended posteriorly between the pelves.

4. DISCUSSION

We consider the orientation of the embryos, i.e. the forward direction of the head and the curvature of the body, as strong evidence against the argument that they are gut contents (Kornhuber 1893). If these tiny lizards were ingested as prey items, they would probably have been swallowed head-first. Once in the gastrointestinal tract, this orientation would have been maintained prior to digestion and disarticulation. Likewise, if swallowed either head-first or tail-first, there would be little chance of enrolment (e.g. embryo number 1; figure 1b,c). Another line of evidence, admittedly negative evidence, for interpreting the small skeletons as embryos, not gut contents, is the absence of skeletal remains of other vertebrates or invertebrates. For example, when preserved in mosasaurs,

gut contents are found as disarticulated masses of bone concentrated in the pelvic region, representing a broad taxonomic cross-section of prey animals (for a review, see Martin & Bjork 1987).

We interpret the advanced (large, highly ossified and fully formed) embryos as an indication that the young were born live, though there is no impartial evidence that parturition occurred underwater rather than on land. While it is possible that *Carsosaurus* laid eggs with near-term embryos, this is unlikely because of physiological and ecological constraints (Andrews & Mathies 2000); almost all egg-laying reptiles oviposit at an early stage (stage 30 of Dufaure & Hubert 1961) (Smith & Shine 1997; Andrews & Mathies 2000) when the embryos are far less developed. The retained embryos of *Carsosaurus* have already reached the size of free-living neonates of living lizards (varanoids) of similar size (figure 2), indicating that they could have been ready to fend for themselves. Finally, no traces of eggshell were found (despite the fine preservation that might have recorded even the parchment shells found in most squamates), suggesting that the young were encased only in soft membranes, as in viviparous forms. We recognize that the absence of eggshell is negative evidence. However, it is significant 'negative evidence' when considered against the embryonic characters of the small skeletons and their finely detailed preservation, as well as the scale impressions of the adult (Kornhuber 1893).

The current specimen thus represents the only fossil record of viviparity in squamates (lizards, snakes and amphisbaenians), a clade in which viviparity has evolved around 100 times (Blackburn 1982, 1985; Shine 1985; Lee & Shine 1998). Among living squamates, viviparity usually characterizes small young clades. Xenosaurid and xantusiid lizards are candidates for the oldest viviparous squamate lineage, but the earliest members of both date from only the Late Cretaceous (Estes 1983; Borsuk-Bialynicka 1988). Thus, viviparity cannot be inferred (based on distribution in living forms) to have existed in any squamates before the Late Cretaceous. Viviparity in mosasauroids such as the mid-Cretaceous *Carsosaurus* might therefore represent not just the only fossil record of the trait in squamates, but also its oldest actual occurrence in squamates. The only other fossil record of viviparity in reptiles is in Triassic (Brinkman 1996; Dal Sasso & Pinna 1996) and Jurassic ichthyosaurs (McGowan 1991), with numerous specimens of *Stenopterygius* (Böttcher 1990) and three specimens of *Ichthyosaurus* (Woodward 1906; Deeming *et al.* 1993).

All four unequivocally identified embryonic skulls point forward, suggesting that the young were consistently orientated. Most marine amniotes that bear young underwater (e.g. cetaceans, sirenians and ichthyosaurs) normally bear their young tail-first, with the nostrils emerging last, to reduce the danger of drowning (Harrison 1969; Böttcher 1990; Deeming *et al.* 1993). The heads-forward orientation of the embryos in *Carsosaurus* is consistent with this. This technique, however, might be more risky than the common head-first method, as reflected by the numerous specimens of embryonic ichthyosaurs that are preserved either mid-parturition or as post-mortem expulsions (McGowan 1991). It is intriguing that an embryo in *Carsosaurus* is preserved within the pelvic-cloacal region, more posteriorly than one would normally expect; this is consistent with the taphonomy of ichthyosaurs (death during parturition, or post-mortem birth). However, some taphonomic disturbance cannot be excluded in this specimen: for instance, the limb element overlying the neural arch has obviously been displaced, and the embryos in the mid-dorsal portion of the body have been disturbed, probably by post-mortem decomposition.

In highly aquatic amniotes, such as ichthyosaurs, cetaceans and sirenians, the young are concentrated anteriorly, freeing the rear body region for propulsion (Böttcher 1990). However, the embryos in *Carsosaurus* are spaced all along the length of the body, as in typical (terrestrial) lizards; this is consistent with morphology indicating only partial aquatic adaptation in *Carsosaurus* (Caldwell *et al.* 1995). Primitive mosasauroids (aigialosaurs) such as *Carsosaurus* were medium-sized (2 m) forms with robust weight-supporting limbs that were only slightly shorter than those of typical terrestrial lizards of similar size (Carroll & deBraga 1992; Caldwell *et al.* 1995). As with living marine iguanas (*Amblyrhynchus*), aigialosaurs were probably competent swimmers also capable of normal locomotion on land. Later, more derived mosasauroids (mosasaurs) possessed flipper-like limbs, fish-like caudal fins and gigantic size (over 10 m), which would have made them incapable of traversing land. Because reptile (amniote) eggs are physiologically incapable of developing underwater (Kennett *et al.* 1993) and derived mosasaurs could not locomote on land, viviparity in these forms could have been predicted. However, the existence of viviparity in their primitive semi-aquatic relatives ('ancestors') could only have been inferred from direct fossil evidence such as the current specimen. The early evolution of live-bearing in these primitive medium-sized aigialosaurs freed them from the need to return to land for oviposition, and would have facilitated the subsequent evolution of larger obligatorily aquatic forms.

REFERENCES

Andrews, R. M. & Mathies, T. 2000 Natural history of reptilian development: constraints on the evolution of viviparity. *Bioscience* **50**, 227–238.

Bell Jr, G. L. 1997 A phylogenetic revision of North American and Adriatic Mosasauroidea. In *Ancient marine reptiles* (ed. E. L. Nicholls & J. Callaway), pp. 293–332. New York: Academic Press.

Blackburn, D. G. 1982 Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphibia–Reptilia* **3**, 185–205.

Blackburn, D. G. 1985 Evolutionary origins of viviparity in the Reptilia. II. Serpentes, Amphisbaenia, and Ichthyosauria. *Amphibia–Reptilia* **5**, 259–291.

Bogert, C. M. & Martín del Campo, R. 1956 The Gila monster and its allies. *Bull. Am. Mus. Nat. Hist.* **109**, 1–238.

Borsuk-Bialynicka, M. 1988 *Globaura venusta* gen. et sp. n. and *Eoxanta lacertifrons* gen. et sp. n.—non-teiid lacertoids from the Late Cretaceous of Mongolia. *Palaeontol. Pol.* **33**, 211–248.

Böttcher, R. 1990 Neue Erkenntnisse über die Fortpflanzungsbiologie der Ichthyosaurier (Reptilia). *Stuttgarter Beiträge zur Naturkunde* B **164**, 1–51.

Brinkman, W. 1996 Ein Mixosaurier (Reptilia, Ichthyosauria) mit Embryonen aus der Grenzbitumenzone (Mitteltrias) des Monte San Giorgio (Schweiz, Kanton Tessin). *Eclogae Geologicae Helvetiae* **89**, 1321–1344.

Caldwell, M. W., Carroll, R. L. & Kaiser, H. 1995 The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. *J. Vertebr. Paleontol.* **15**, 516–531.

Calligaris, R. 1988 I rettili fossili degli 'Strati calcariei ittilitici di comeno' e dell'isola di lesina. *Atti del Museo Civico di Storia Naturale Trieste* **41**, 85–125.

Carroll, R. L. & deBraga, M. 1992 Aigialosaurs: mid-Cretaceous varanoid lizards. *J. Vertebr. Paleontol.* **12**, 66–86.

Dal Sasso, C. & Pinna, G. 1996 *Besanosaurus leptorhynchus* n. gen. N. sp., a new shastasaurid ichthyosaur from the middle Triassic of Besano (Lombardy, N. Italy). *Paleontologia Lombarda, Nuova Serie* **4**, 3–23.

deBraga, M. & Carroll, R. L. 1993 The origin of mosasaurs as a model of macroevolutionary patterns and processes. *Evol. Biol.* **27**, 245–322.

Deeming, D. C., Halstead, L. B., Manabe, M. & Unwin, D. M. 1993 An ichthyosaur embryo from the Lower Lias (Jurassic: Hettangian) of Somerset, England, with comments on the reproductive biology of ichthyosaurs. *Mod. Geol.* **18**, 423–442.

DeLisle, H. F. 1996 *The natural history of monitor lizards*. Malabar, FL: Kreiger.

DuFaure, J. P. & Hubert, J. 1961 Table de développement du lézard vivipare: *Lacerta* (*Zootoca*) *vivipara* Jacquin. *Archives de Anatomie, Microscopie et Morphologie Experimentale* **50**, 309–328.

Estes, R. 1983 *Handbuch der paläoherpetologie. 10A. Sauria terrestria*. Stuttgart, Germany: Gustav Fischer Verlag.

Harrison, R. J. 1969 In *The biology of marine mammals* (ed. H. T. Andersen), pp. 253–348. New York: Academic Press.

Kennett, R., Georges, A., Palmer-Allen, M. 1993 Early developmental arrest during immersion of eggs of a tropical freshwater turtle, *Chelodina rugosa* (Testudinata: Chelidae), from Northern Australia. *Aust. J. Zool.* **41**, 37–45.

Kornhuber, A. G. 1893 *Carsosaurus marchesetti*, ein neuer fossiler Lacertilier aus den Kreideschichten des Karstes bei Komen. *Abhand Lungen der Geologischen Reichsanstalt Wien* **17**, 1–15.

Lee, M. S. Y. & Shine, R. 1998 Reptilian viviparity and Dollo's law. *Evolution* **52**, 1441–1450.

McGowan, C. 1991 *Dinosaurs, spitfires and sea dragons*. Cambridge, MA: Harvard University Press.

Martin, J. E. & Bjork, P. R. 1987 Gastric residues associated with a mosasaur from the late Cretaceous (Campanian) Pierre Shale in South Dakota. *Dakoterra*, **3**, 68–72.

Shine, R. 1985 The evolution of viviparity in reptiles: an ecological analysis. In *Biology of the Reptilia. 15. Development B* (ed. F. Billett), pp. 607–694. New York: Wiley.

Smith, S. A. & Shine, R. 1997 Intraspecific variation in reproductive mode within the scincid lizard *Saiphos equalis*. *Aust. J. Zool.* **45**, 435–445.

Woodward, A. S. 1906 On two specimens of *Ichthyosaurus* showing contained embryos. *Geol. Mag.* **3**, 443–444.